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COMPARATIVE MORPHOLOGY OF THE EAR.

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COMPARATIVE MORPHOLOGY OF THE EAR.

FOURTH ARTICLE.

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It is generally believed by entomologists that insects can hear. Indeed, the sounds produced by many species appear to be sexual calls, by which the males endeavor to attract the opposite sex, which must therefore hear. All attempts, however, to demonstrate the existence of an auditory organ in insects have hitherto failed. The only organs which might be interpreted as answering functionally to an ear are the so-called tympanal organs of Orthoptera, but it has never been demonstrated that these peculiar structures do really subserve the sense of hearing. Nevertheless they are commonly considered to do so, and in accordance with the prevalent view, which I am by no means prepared to accept, it will be appropriate to give an account of the organs in question.

8. The Tympanal Organs of Orthoptera, and Allied Structures in other Insects.

The so-called tympanal organs of grasshoppers and crickets were known to entomologists in the early part of this century, for they are mentioned in the manuals of entomology by Burmeister, and by Kirby and Spence. The singular structures connected with them were first discovered by Johannes Müller (VII.), and were subsequently investigated with great skill and success by his distinguished pupil, C. Th. von Siebold (IX.). Since then our knowledge has

been enlarged by contributions from Leydig (IV., V., and VI.), Hensen (III.), and Oscar Schmidt (VIII.). More recently still Graber has published an elaborate monograph (II.) with ten quarto plates. This last memoir is very valuable, and although the histological part leaves much to be desired, it may fairly be termed exhaustive in its general treatment. It is, however, marred by prolixity so extreme that the memoir could easily have been reduced to one third, and might, possibly, have been reduced to one sixth, of its present dimensions without omitting any of the results. A considerable proportion of the unnecessary part of the text consists of descriptions of the mistakes made by the author, and diffuse explanations of how he fell into them. It is not an uncommon error to report the accidents as well as the results of a research, although they are due only to personal causes, and, therefore, not obstacles to be pointed out to others. This criticism may be applied quite generally to German scientific writings, which are notoriously so often defective in form and style that it is time to blame them and demand improvement, since it is, perhaps, not too much to say that there is no nation whose contributions to science are so badly written as the German.

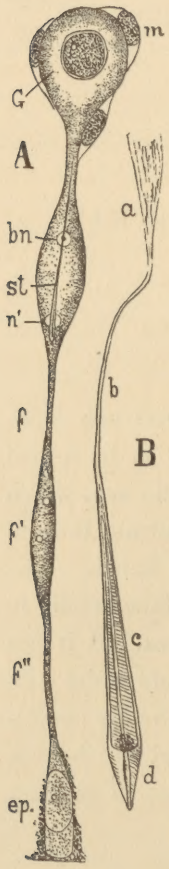

FIG. 21. Locusta viridissima. A, terminal body of the supratympanal organ. *G*, ganglion cell, and its membrane, *m*; *bn*, basal nucleus; *st*, rod; *n'*, top nucleus; *f*, *f'*, *f''* peripheral fibre; *ep*, epidermal cell.

B, isolated rod; *a*, its commencement; *b*, thread; *c*, body; *d*, head. After Graber.

The essential parts of the structures we are to consider are the peculiar terminal organs, which end the nerve fibres of the structures. Each of the terminations in question is an elongated continuation of the nerve fibre, consisting of three parts: 1, a proximal ganglion cell; 2, a middle swelling containing a stiff rod; 3, a distal fibre running to an epidermis cell. The fibre is apparently wanting in certain cases, there being then no connection with epidermis. These divisions of the organ are shown in Fig. 21, A,

which represents one of the nerve terminations, taken from the supratympanal cluster in the foreleg of the katydid, *Locusta viridissima*. *G* is the ganglion cell, with large round nucleus; it is enclosed in a special cellular sheath *m;* the connection of the ganglion cell with the nerve fibre is not shown, but in other views the two poles would both be seen, one uniting with the nerve, the other extending, as in the figure, to make the middle enlargement, containing the rod (*Stift*), *st*, and usually two nuclei, *bn* and *n'*, but in some species the nucleus *bn*, nearest the ganglion cell, is wanting; the peripheral fibre, *f*, *f'*, *f''*, is quite long, a little thickened in the middle, and united by its outer end with the basal process of an epidermal cell, *ep*, which last is, of course, part of the skin of the leg. The rod, *st*, extends throughout the entire length of the middle enlargement; a rod, more highly magnified, is shown in Fig. 21, B, — it begins towards the ganglion cell in a manner not clearly determined, but quickly appears as a distinct thread, *b*, which passes into a conical thicker portion, *c*, to finally end off in a head, *d*, which is pointed like an inverted pyramid.

With a single exception, which will be described immediately, the type of terminal organ just presented to the reader is characteristic of the Orthoptera, and reoccurs, as far as the observations at present avail for forming a judgment, with no important modifications in other orders of insects. Unfortunately the range of variation is reserved through our present ignorance for future determination.

The only departure from the described type that can now be presented occurs in the terminal organs which lie upon the wall of the trachea or air tube in the leg of the katydids (*Locustina*), see Fig. 22, representing a section through the wall of the trachea; *m'* is a membrane forming part of the wall of the trachea; *n'* is distal nervous fibre running from the ganglion cell, not included in the drawing;

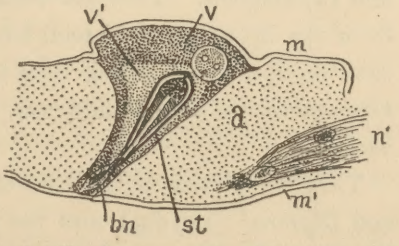

Fig. 22. Transverse section of Siebold's or the intra-tympanal organ of Locusta. *bn*, basal nucleus; *st*, rod; *m'*, membrane of trachea; *n'*, fibre from ganglion; *m*, *Deckmembran;* *v*, outer, *v'*, inner vesicle. After Graber.

the connection of the ganglion pole, *n'*, with the rod vesicle is wanting in this section, but can be seen in Fig. 26. The vesicle is placed nearly at right angles with the fibre, and is triangular in outline, the apex pointing downwards and uniting with the fibre. The rod, *st*, is much shorter and thicker than in the other form, and is surrounded by a clearer space, *v'*, like an inner vesicle, which again is bounded by a darker part or outer vesicle, *v;* the latter bears the small basal nucleus, *bn*, and a larger round nucleus with two nucleoli in the upper part. The whole is covered by a membrane, to which we shall recur. What fills the space, *a*, around the terminal organ is not satisfactorily determined. Especially noteworthy is the absence of any distal continuation of the rod-bearing vesicle.

According to Graber's descriptions the entire "*Endorgan*" is a continuous protoplasmatic mass with multiple nuclei. Now one adequately familiar with histology cannot regard this as probable, but must consider that each nucleus belongs to a distinct cell, and that the apparent absence of discrete cell boundaries is to be attributed to the imperfection of Graber's observations. Hensen states that each rod is surrounded by four cells, a *Deckzelle*, two *Seitenzellen*, and a *Basalzelle*, but his description seems to me not consistent with itself throughout.

These rod-bearing terminal organs have not been found in any of the Arachnida or Myriapoda, but only in the true or six-footed insects. They have been observed in *Orthoptera*, *Coleoptera*, *Diptera*, and *Lepidoptera*. They are usually situated in or near the thorax or in the appendages thereof, forming in each species two symmetrical groups. Concerning their occurrence in any order except the Orthoptera, we possess, however, only extremely fragmentary observations.

They are placed in the base of the hind wings among *Coleoptera* and *Diptera*[1] (Leydig), and the spot occupied by them is indicated by certain modifications of the overlying epidermis. This spot had been observed in Diptera, but falsely described by Hicks.[2] It is

[1] In the Diptera the hind wings are rudimentary, and are termed *halteres*.

[2] Hicks, J. B.: Proc. Linn. Soc. Zool., I., 1857, and Trans. Linn. Soc., London, XXII., 1857.

characterized by wide pore-canals through the cuticula, closed externally by a thin membrane bearing a tiny hair or wart. Probably there is a special cell under each pore, and each cell connected with a rod-bearing terminal organ, since there appears to be a rod corresponding to each pore-canal. The whole structure is underlaid by a dilatation of an air-tube (trachea). Leydig gives (IV., 299–310) a few details, but we miss minuter and more extended accounts. It is interesting to see that these terminal organs may occur without any tympanum-like modification of the epidermis, so that here there is nothing to suggest that they have an auditory function.

Concerning *Lepidoptera* we possess only fragmentary observations. A. H. Swinton claims to have found a distinct tympanal organ in first abdominal segment of several moths, but his description employs a very antiquated terminology, which is a little confusing. There is on the side of the anterior and constricted portion of the first abdominal segment a smooth oval membrane, which appears to be homologous with the tympanum of the Acridians, which we shall describe presently. The adjacent interior of the segment is occupied by very complicated air-cells. A spiracle lies *behind* the membrane (not in front as in the grasshoppers). A nerve passes from the third thoracic ganglion "obliquely across and round the elevator muscle of the hind wing" to the supposed tympanum, where it is connected with a structure (Swinton's "membranous vesicle"), which is apparently identical with the structure in like position in the grasshoppers, which latter was likewise originally described as a vesicle, but is now known to be really a cluster of rod-bearing terminal organs. Underneath this structure is a thickening of the cuticula, as in Orthopterous forms. It is probable that this organ in moths is entirely homologous with that of the Acridians, but the matter must remain uncertain until the terminal rods have been found on the Lepidopterous tympanum.

Among *Orthoptera* they appear in two distinct localities, namely in the grasshoppers on the side of the first abdominal segment, in the crickets (*Gryllodea*) and katydids (*Locustina*) in the upper part of the third joint or tibia of the fore legs. In both cases the surrounding parts have undergone modifications, which, in conjunc-

tion with the terminal bodies proper, make the so-called tympanal organs.

We begin with the organ of grasshoppers. It consists of three parts; the tympanum proper, which is a modified portion of the integument; the cluster of rod-bearing organs; and, finally, a vesicular enlargement of the underlying trachea.

The tympanum lies upon the side of the first segment of the abdomen, immediately behind the spiracle (Fig. 23). It is oval in outline, but sometimes presents a hilus upon the side towards the spiracle, thus becoming reniform, as in *Rhomalea*. Its outer surface is glistening and much smoother than the surrounding skin or crust. Its lower and anterior quarter is slightly roughened, usually by furrows, which run obliquely downwards and backwards; this quarter also carries hairs in a few species. The crust around its margin forms a thickened ring, which projects on the inner surface, and is not continuous, but interrupted at the lower edge of the tympanum (Fig. 23, V). — The tympanum may lie nearly on a level with the surface of the body, or be sunken below it; in the latter case the marginal ring becomes more prominent and complicated, especially by the development of folds, which, in a certain series of forms (Graber, II., 85–87), increase more and more until they cover over most of the tympanum (e. g., *Stenobothrus*, *Pachytylus*). The cuticula of the tympanum is thinner than that of the unmodified epidermis, and offers two specialized parts for consideration. The largest (Fig. 23, *l' l''*) is termed the "*zweischenkeliges Körperchen*" (two-shanked corpuscle), and lies nearest the spiracle, *sp*. It has three components: the central body, *k*, and the two legs, *l' l''*. The central portion projects inwards, and is really an invagination of the cuticula, for it is a hollow knob opening directly to the outside by a fine canal. The upper leg, *l'*, is a rod-like thickening of the inner

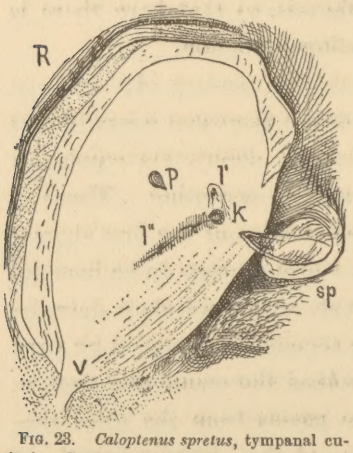

Fig. 23. *Caloptenus spretus*, tympanal cuticula. *R*, ring; *sp*. spiracle; *p*, pear-shaped body; *l'*, *k*, *l''*, *zweischenkeliges Körperchen*.

surface of the cuticula; its upper end broadens and thins out, while its lower end forks to embrace the central body. The lower leg, *l''*, runs obliquely backwards, and is formed by two ridges with a shallow furrow between, the posterior ridge being much higher than the anterior; the cuticula over the furrow bulges out a little, but is not much thickened. The second part, the pear-shaped body (Fig. 23, *p*), is usually present, and lies near the centre of the tympanum. The small end of the pear points inwards towards the ganglion tympani. This body is a thickening of the cuticula, and is traversed by fine pores. Its total absence in some forms (*Rhopalonema* and *Tropidarcis*) indicates that it is not a necessary part of the tympanal apparatus. The epidermis under the cuticula of the drum is composed of a single layer of thin, polygonal cells with large, clear nuclei. Leydig wrongly asserted that the cells extended over a part only of the tympanum. The cells contain pigment under the front part and under both the thickened portions of the cuticula of the drum.

The tympanum is wanting in the Proscopidæ, Mastacidæ, Tryxalidæ, and Tettigidæ.

Graber describes under the name of *Tensor tympani* a flat bundle of twenty or more muscular primitive fibres, which arise from an inner process of the crust just below the stigma in front of the tympanum, and run downwards.

We pass to the terminal organs proper. The epidermal cells under the "*zweischenkeliges Körperchen*" and the pear-shaped body (Fig. 23) are, mostly, if not all, prolonged at their bases into a tapering process, which unites with an *Endorgan*, as before described. (Fig. 21.) These bodies all extend towards the mass of ganglion cells placed over the "*zweischenkeliges Körperchen*," and from this passes off the nerve to its origin in the third thoracic ganglion. The result of the arrangement described is that the cluster of parts presents the following appearance when viewed from the inner surface, after the removal of the tracheal vesicle; the nerve, Fig. 24, N, ascends towards central body, Fig. 23, *k*, before reaching which it expands into the ganglion Fig. 24, *G*, which is enclosed in a pig-

mented envelope, and is divided into a larger upper part and a smaller inferior portion. The main mass of the terminal organs, *T*, appear as the direct continuation of the ganglion, and form with it a pyramidal body, the apex towards the nerve; the base of the pyramid has two extensions, one, *p*, consisting in all the species that have been examined of seven terminal organs, running out to the pear-shaped body; the second, *s*, ascending along the vertical shank of the "*zweischenkeliges Körperchen.*" The smaller division of the pyramid contains the *Endorgans*, *f*, which spread out along and down the inferior furrowed extension of the "Körperchen." Of course those rod-bearing structures which occupy the periphery and the extensions of the pyramid are longer than those in the centre. In form these *Endorgans* differ but slightly from the type shown in Fig. 21.

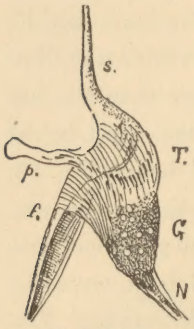

FIG. 24. *Pachytylus stridulus*, tympanal *Endorgan* isolated. *N*, nerve; *G*, ganglion; *T*, terminal organs; *p*, terminal organs of pear-shaped body; *s*, of vertical shank; *f*, of lower shank. After Graber.

Two tracheal vesicles, or air sacks, lie on each side under the tympanum, and are developed from branches of the trachea arising from the tympanal stigma. As far as known they have no special connection either with the tympanum or the terminal organs.

We turn now to the study of the tibial tympani of locusts and crickets, which are found, as above stated, in the upper part of the third joint of the fore legs. If we imagine the leg stretched out horizontally at right angles to the body, the upper side would be that termed the hæmal, the lower the neural, and we should also distinguish the anterior and posterior surfaces.

If the fore-tibia of a green locust or katydid be examined, there will be found on the upper surface near the end towards the body two narrow slits, Fig. 25, *a;* a transverse section through them is represented in Fig. 26. The slits are seen to lead into narrow fissures; the outer walls formed by mere flaps, *a* and *b*, the inner walls being two membranes; the anterior, *ty*, and posterior, *ty'*, tympana. The space between the two tympani is occupied by two large air-sacks or tracheal vesicles, one anterior, *Tr. a*, the other posterior,

Tr. p. The vesicles divide the lower part of the section from the upper; the former contains several muscles, *m* 1, *m* 2, *m* 3, nerves, *n* and *n'*, a tendon, *s*, and other tissues. The upper part contains principally connective tissue and the terminal organs, which particularly concern us. They, *so*, lie against the wall of the anterior trachea, forming a row along the upper surface of the air-tube, each with its accompanying ganglion cell, *sg*. An enlarged section of these terminal organs has been already described and figured (Fig. 22). If the anterior trachea be isolated and viewed from the hæmal side, it presents the appearance of Fig. 27. The nerve, *N*, runs along, expanding to a ganglion just before reaching the level of the external tympanal fissures, which are connected with a special cluster, the supratympanal of terminal organs, *st*. The nerve then continues along the anterior edge of the trachea, forming the elongated Siebold's ganglion, *sg*, each cell giving off an oblique fibre, *n'*, which goes to one of the *Endorgans*, *S*, as previously described. These last make the so-called Siebold's or intratympanal organ, which begins with a cluster of rod structures, *S'*, and is continued as a single row of terminal organs, which grow smaller and smaller until at the distal end they are very minute. The intratympanal organs are found only in the Locustinæ.

FIG. 25. *Locusta viridissima*. Tibia of fore-leg. *a*, slits leading into the tympanal fissures. After Graber.

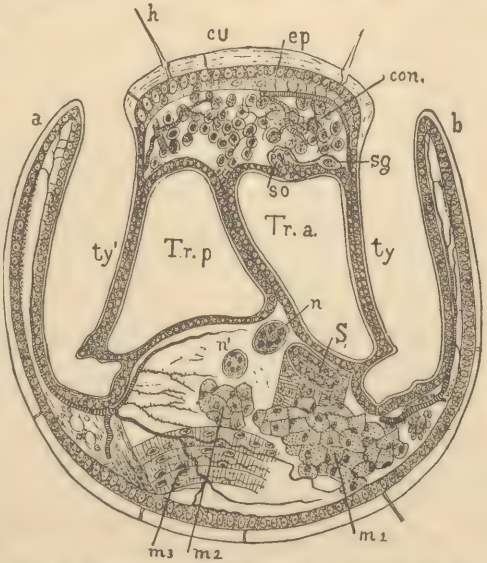

FIG. 26. *Locuesta viridissima*. Section of tympanal region of fore-leg. *h*, hair; *cu*, cuticula; *ep*, epidermis; *conn*, connective tissue; *sg*, Siebold's ganglion; *so*, Siebold's terminal organ; *a*, *b*, tympanal cover; *ty*, anterior, — *ty'*, posterior tympanum *Tr. a*, anterior, — *Tr. p*, posterior air-sack; *n*, *n'*, nerves; *S* tendon; *m* 1, *m* 2, *m* 3, muscles. After Graber.

A section (Fig. 28) through one fork of the supratympanal organs

(*st* of Fig. 27) shows their different arrangement. The supratympanal organs occur in both locusts and crickets; the actual figure is from a cricket. The ganglion, *gl*, is spread out underneath the epi-

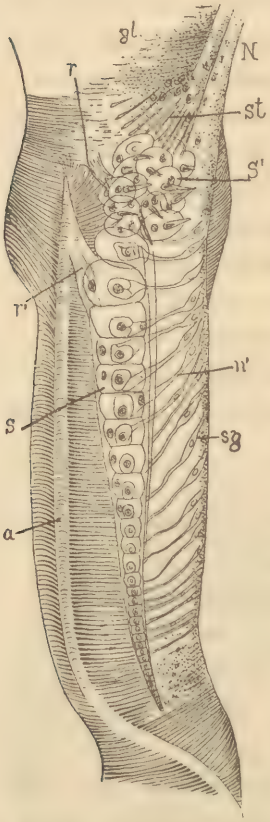

FIG. 27. *Ephippigera vitium.* View of outer or hæmal surface of anterior trachea of fore-leg, to show Siebold's Endorgan. *gl*, supratympanal ganglion; *N*, nerve; *st*, supratympanal terminal rods; *S'*, *S*, Siebold's organ; *n'*, distal thread from cell of Siebold's ganglion, *sg*; *a*, ridge on trachea; *r*, *r'*, roots of the covering membrane. After Graber.

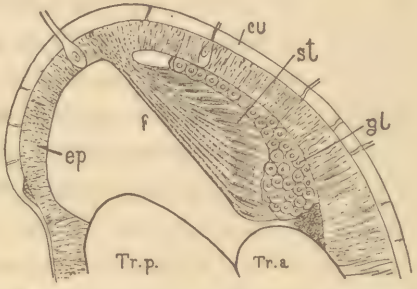

FIG. 28. *Gryllus campestris.* Section of epidermal branch of supratympanal organ. *ep*, epidermis; *cu*, cuticula; *st*, terminal organs, with their distal thread, *f*; *gl*, ganglion.

dermis, on the hæmal side (*i. e.* above, when the leg is horizontal) of the anterior trachea, *Tr. a.* From the ganglion spring the rod-bearing bodies, *st*, each of which gives off a thread, *f*, which runs across and unites with a basal process of an epidermal cell. In the figure only the general fusion of the threads and epidermis is shown. The peculiar disposition of the threads, by which their length is varied like the wires in a piano, can be best understood from the figure. Fig. 21 represents an isolated supratympanal terminal organ.

To complete our description we have to add certain details and an account of the variations occurring in different species.

The folds which cover the tympana are secondary structures, which are wanting in young katydids. They are often absent, or again one cover and not the other is developed. Species of the same genus vary in this respect. Around the tympanum the cuticula is thickened to form a complete or nearly complete ring, and over the tympana the cutic-

ula is thin with few pores and hairs, and a finely sculptured external surface. In all Gryllacridæ and some Stenopelmatidæ the tympana are wanting, but in all other Locustinæ both are present; among the Gryllidæ, all the chirping forms have a tympanum, but the mute forms do not; in some species the two tympana are unlike in structure, and often one tympanum is rudimentary, or altogether wanting, as in Gryllotalpa the posterior, in Platydactylus, Gryllus, etc., the anterior. Most species of crickets have a large posterior and small anterior tympanum. The terminal organs are present when the young insect is hatched from the egg, but the tympana are not well marked until after three or four moults, and the covering flaps are developed still later in the Locustinæ; in crickets the development is even more retarded. The development of the tracheal vesicles follows that of the tympana, both in time and extent, so that when the tympanum is small the adjacent vesicle is small, and when the former is wanting the latter is also.

The supratympanal ganglion and organ is really bipartite, and the account given above refers in fact only to that branch, the anterior and larger, which lies under the epidermis. (Fig. 28.) The other part extends transversely over the wall of the anterior trachea, but has not yet been carefully studied.

The supratympanal organ exhibits the following features requiring mention. The rods (Fig. 21, B) consist of a thread, a gradually thickening body, and a pointed head. The head and body are said to be traversed by a central canal into which extends the thread; the rods consist of homogeneous core and a more highly refractile envelope, with four ridges projecting inwards; in transverse section the rods present a rounded circumference. The entire organ is covered by a thin membrane, stated to be an extension of the neurilemma and of the basement membrane of the epidermis.

Siebold's, or the intratympanal, organ, which it will be remembered is found only in the Locustinæ, and in none of the order of crickets, is especially characterized by the modified form of the rods, the absence of threads connecting with the epidermis, the peculiar arrangement of the terminal structures, and the regularly progressing diminution of size towards the distal end. The ganglion cells are

very easily seen to be bipolar, their distal pole being a quite long thread. The number of terminal organs in the straight row (Hensen's *crista acustica*) is at least thirty-three in Locusta and twenty-eight in Ephippigera. The top-shaped rods are round and not quadrilateral as supposed by Leydig; they have a central canal and thread, and Graber asserts that their lower pointed end is united with the axis-cylinder from the ganglion cell. The basal nucleus of the terminal organ (Fig. 22, *bn*), resembles a nerve nucleus. The superior nucleus (Fig. 22) is much larger, spherical, and has two evident nucleoli; in Locusta there are two of them, in other genera only one.

A few additional details, but nothing, so far as I am aware, of great importance, has been omitted. The preceding accounts show that we have to do with unquestionable sense organs, although of a very unusual character. The nerve fibre ends in a ganglion cell, which is connected with a multicellular organ, especially characterized by the presence of a tapering rod. These singular structures are always found overlying an air sac, and in most cases (possibly all) are organically connected with epidermal cells by uniting threads. The presence of the tympana is secondary, since they are wanting in some imagos, and in the young stages of those species in which in the adult condition they are found. As to their possible function we possess no satisfactory indication; but it seems particularly improbable that they are auditory organs.

They occur very widely among insects, and it is to be expected that further investigation will show that their distribution is more general than has been hitherto usually assumed. It is certain that they are of much importance, but their physiological rôle is, we repeat, unknown.

A list of the authorities consulted is subjoined.

In the next article we shall begin with the morphology of the vertebrate ear.

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